Chapter 29

FUNGAL TAXA, PHYSIOLOGICAL GROUPS, AND BIOMASS: A COMPARISON BETWEEN ECOSYSTEMS

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I. INTRODUCTION

Fungi in the form of yeasts, mushrooms, toadstools, and molds have occupied man's general interest for a long time. However, scientific investigation of fungi, especially invisible soil fungi, is a relative newcomer to biological sciences, the work of Adametz (1886) being the starting point for serious soil mycological studies. The communications of Jensen (1912) and Waksman (1916a,b, 1917) ask the question as to whether there is any fungus flora of the soil and further attest to the recency of soil mycological studies. Adametz and several others including Reinitzer (1900) and Nikitinsky (1902) studied their isolates for clues to their biochemical or ecological role in soil.

As soon as soil fungi were accepted as natural entities in soils, their role therein became of interest, especially to those investigating soil fertility. Thaysen and Bunker (1927) presented a comprehensive review of the activities of fungi in hydrolysis of cellulose, hemicellulose, pectin, and gums.

During more recent years numerous publications have proven the ubiquitous occurrence of fungi in soils. Lists of taxonomic groups within and between different soils are common to the literature of fungal ecology, i.e., mycoecology. But taxonomic listings tell us little of the role played by soil fungi in ecosystem development and maintenance and nothing of the composite fungal niche in ecosystems.

From the beginning of the twentieth century fungal activities in the soil have been discussed and investigated in relation to their role in ammonification, nitrification, nitrogen transformation, cellulose decomposition, and humification. These investigations concerned themselves with organisms isolated from the soil. The methods and approaches used in different sites by different workers varied, thus forestalling comparative studies among different soils. Until Jones and Mollison (1948), soil fungi were quantified in terms of the number of their occurrences on soil dilution agar plates. The inadequacy of such quantification need not be stressed here, but it should be pointed out that the use of the soil dilution isolation technique for fungi probably led to the generally held concept that soil bacteria were the

major components of soil microfloras and were the main agents in organic decay and nutrient cycling processes.

The range and magnitude of metabolic capabilities for invisible soil microorganisms have been constructively reviewed recently by Clark (1975). As the number of reports multiply it is becoming established that fungi, not bacteria, are the major constituents of soil microfloras (Anderson and Domsch, 1973; Satchell, 1974; Flanagan and Van Cleve, 1977). Because of the high relative activity of microorganisms [i.e., the ratio of energy flow to biomass, which has been estimated to be as high as 1000 (Odum, 1968)], it is obvious that study of major soil microorganisms is essential to an understanding of ecosystem function and soil fertility.

The biomass of fungi in soil is not easily measured. It is possible to determine the length of fungal filaments per gram of mineral soil or litter, but the proportion of live and dead hyphae in substrates is not so easily resolved. These problems have been discussed most recently by Frankland (1974, 1975) and Söderström (1977). The problems of "ghost hyphae" (Frankland, 1974) and the resolution of live hyphae may be overcome by the addition of 2% aceto-orcein, a nuclear stain, to the material being examined prior to using either the method of Hanssen et al. (1974) or that of Jones and Mollison (1948) (see Sec. II).

Fungal biomass expressed as meters of hyphae per gram of soil or as grams per square meter shows wide spatiotemporal variation within ecosystems (Flanagan and Van Cleve, 1977; Söderström, 1977; Bunnell et al., 1978). Temporal variation is greatest in the spring and fall in high latitude sites, presumably through stimulation from incoming nutrients and nonstructural carbon compounds. Studies which did not use some method to distinguish live from dead fungal hyphae do not show the seasonal fluctuation in fungal biomass (Nagel-de Boois and Jansen, 1971). Expressing fungal biomass in meters per gram of dry weight soil (DWS) without regard to the quantity of organic matter involved must be misleading.

In the following discussion I will attempt to deal with the detectable fungal components from seven widely separated and different soils, both in terms of their potential to decay substrates and in terms of their biomass in relation to stated variables such as the quantity of organic matter. I hypothesize that different microbial taxa from various soils do not show significant differences in their capabilities for attack of indigenous plant residues. Thus, a universal decomposer system exists whose member microorganisms differ from place to place but whose specific catabolic capabilities enable it to decay all natural organic residues, limited only by climatic extremes and by substrate availability. The latter constraint will be reflected in the dimensions of the decomposer community, i.e., the microbial biomass and its turnover rate. Turnover rate, or generation times, will not be discussed here, but work on this important aspect of microbial ecology has begun and is reported in Babiuk and Paul (1970), Gray and Williams (1971), Flanagan and Bunnell (1976), and Flanagan and Van Cleve (1977).

II. STUDY SITES AND METHODOLOGY

A. Study Areas

The sites were selected more by coincidence than by design. Investigations were carried out in Alaska concurrent with U.S. International Biological Program (US/IBP) tundra investigations, National Science Foundation (NSF) sponsored research on taiga ecosystems, and oil industry sponsored research on taiga forest areas. Two temperate sites, a grassland and a sphagnum-peat bog site in western Ireland were examined during 1974-1975 while the present author was at Galway University.

The site at Pt. Barrow, Alaska (71°18'N, 156°40'W), was in the US/IBP Tundra Biome intensive research area. This site is described in detail by Bunnell et al. (1975). The study plots were covered by an almost pure stand of *Eriophorum angustifolium*.

The Alaskan Eagle Summit site, also a US/IBP Tundra Biome site, situated at 65°28'N and 145°23'W, has been described by Anderson (1974). The microbiological investigations were performed in a pure stand of *Dryas octapetala* at 1200 m in an alpine tundra environment.

Study sites in interior Alaska included a black spruce forest (*Picea mariana* [Mill] B.S.P.), an aspen forest (*Populus tremuloides*), and a paper birch forest (*Betula papyrifera*).

The black spruce forest floor is covered with *Hylocomium spendens* and frequent patches of *Pleurozium schreberi* and *Sphagnum* sp. Emergent from moss layers, *Ledum groenlandicum* and an occasional *Rosa acicularis* compose the shrub layer. *Vaccinium vitis-idaea* and *Oxycoccus macrocarpus* are the dominant herbaceous forms.

The aspen stand was typical of those on south-facing slopes in interior Alaska. Bear berry (*Arctostaphylos uva-ursi*) was dominant in the understory and occasional willows in lower reaches of the stand. *Viburnum* sp. occurred occasionally.

The paper birch stand contained *Alnus* sp. intermingled with the major trees. Open areas between trees were dominated by *Calamagrostis*, while the entire forest floor was covered by *Equisetum arvense*. Patches of *Hylocomium splendens* occurred among the *Equisetum*.

The temperate sites studied were both in western Ireland. A limestone subtended grassland site was selected on the western bank of Lough Corrib, about a half mile (ca. 0.8 km) north of Galway University. *Festuca* spp. accounted for approximately 70% of plant cover, while *Trifolium repens*, *Ranunculus repens*, and *Agrostis tenuis* made up the remainder. In this site flushes of *Pteridium aquilinium* occurred occasionally where the meadow abutted walls or alder thickets.

A temperate peat bog (blanket bog) approximately 30 miles (ca. 48.6 km) west of Galway City in the Maam Valley was studied between April and November. The peat, which never freezes to a significant depth or for much time, is permanently waterlogged, averages 2-5 m depth, and is frequently interrupted by small (1-10 m diameter) bog pools containing acidic water. Ericaceous shrubs including *Calluna vulgaris*,

Erica tetralix, and *E. cinerea* predominate. *Eriophorum angustifolium*, *E. vaginatum* and *Scirpus caespitosus* are the primary graminoids on the less wet areas, while wetter spots and pool margins contain *Juncus effusus*, *Schoenus nigricans*, and *Molinia caerulea*. The bryophyte community is composed predominately of *Sphagnum* spp.

The study sites, all in the Northern Hemisphere, occur between the latitudes 55° and 72°. There is a wide range in annual patterns of air temperature between sites (Table 3), and annual precipitation across sites varies between 1300 mm (temperate peat bog) and 124 mm (Pt. Barrow tundra), the mean between extremes, 675 mm, occurring at the Eagle Summit site.

B. Isolation of Fungi and Enzyme Hydrolytic Capability

Fungi were isolated from standing dead gramineous leaves and from L, F, H, and A_1 soil horizons, where such were discernible, using the particle-washing technique of Parkinson and Williams (1961). Fungi were not isolated from tree leaves until they had fallen as litter. In order to detect seasonal colonization patterns, fungal isolations were made at each site from all plant residues and soil horizons at four separate times throughout at least one field season.

Identification of fungal isolates was carried out in our own laboratories, and further identification and confirmation was provided through the help of the staff of the Centraalbureau voor Schimmelcultures, Baarn, Netherlands. Percent frequency of an isolate was calculated as follows:

$$\frac{\text{number of plated particles producing a species}}{\text{total number of particles plated}} \times 100$$

Fungal enzyme content and capability to degrade cellulose, pectin, starch, humic acid, and gallic acid were measured as described by Flanagan and Scarborough (1974).

Lignocellulose dowels were powdered by shaving them in pencil sharpeners and then passing them through a Wiley mill. The powdered lignocellulose was the sole carbon source in a mineral salt agar layer poured as a thin overlay on plain agar medium. Organisms capable of degrading lignin and cellulose in combination will clear a zone among the closely crowded wood particles. Ability to utilize xylan was measured in the manner described by Domsch and Gams (1969). Organisms giving positive responses at room temperature were examined for the same activity at 2-5°C.

Species which together accounted for >80% of all species were considered the major species components (exclusive of basidiomycetes). In-site potential in a decomposition characteristic, e.g., cellulose decomposition ability was calculated:

$$\frac{\text{frequency sum of species with a given activity}}{\text{frequency sum of major species components}} \times 100$$

C. Biomass Estimates

Site fungal biomass was measured using several techniques. From 1970 to 1974 the methods of Jones and Mollison (1948) were used at the Barrow, Eagle Summit, and Fairbanks sites. At the temperate grassland and bog sites, fungal biomass was measured using the technique of Hanssen and colleagues (1974). To distinguish live from dead

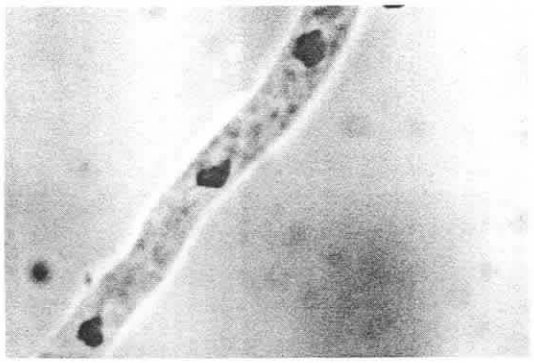

Fig. 1 Fungal hypha in slide stained with aceto-orcein. Width of hypha = 1.8 µm.

hyphae an aceto-orcein stain was included in the application of the two techniques used. Aceto-orcein (2.0 g in 100 ml of 10% acetic acid) was added to the fresh soil sample prior to conventional application of the Jones and Mollison (1948) and Hanssen et al. (1974) techniques. Aceto-orcein stains fungal mycelium a light reddish color, and nuclei are seen as densely stained spheroids (Fig. 1). The assumption was that the presence of cytoplasm and especially cytoplasm with nuclei in hyphae indicated live mycelium. Results with the aceto-orcein technique as applied to tundra soils were compared with estimation of live fungal biomass in the same soils using Frankland's (1974) technique. Results of both techniques were significantly correlated ($P < 0.05$).

D. Cellulose Decomposition Studies

At each of the study sites cellulose strips, 10 cm long, composed of acid-washed Watman No. 1 filter paper, were placed vertically in the upper 10 cm of earth. Cellulose decay rates within and differences between latitudinally separated sites were measured by determining weight losses in 20-30 strips collected at each site after a 90-day interval.

III. RESULTS

A. Mycofloral Taxonomy, Enumeration, and Distribution

It is not my purpose here to describe or compare the fungal taxa recovered in each study site. However, examples of taxonomic data are shown in Tables 1 and 2 for the reader's information and to clarify the means by which the data presented in the figures were calculated. Lists of species and their enzyme activities for the Pt. Barrow and Eagle Summit sites may be found in Flanagan and Scarborough (1974) and Bunnell et al. (1980). The isolates obtained in the Fairbanks aspen forest and those from the temperate bog site were not as carefully identified as those reported presently and by Flanagan and Scarborough (1974). Dowding and Widden (1974) report in detail on the fungi in a similar peat bog in western Ireland, and the taxa of fun-

Table 1 Taxonomy, utilization potential and frequency (%) of fungi in a temperate-grassland site[a,b]

Organisms	Standing dead in phyllosphere	Litter	Soil 0-10 cm	Soil 10-20 cm	Activity on: Pectin	Starch	Xylan	Cellulose	Humic acid	Gallic acid	Wooden dowels (lignocellulose)
Phycomycetes											
Circinella sp.	1.0	1.7			+	+	-	-	-	-	-
Mortierella elongata	2.3				+	+	+	-	-	-	-
M. pusilla	2.6		4.6		-	+	+	-	-	-	-
M. (cf.) *ramanniana*	2.8	3.0			-	+	+	-	-	-	-
Mucor spinescens	3.4	2.7		2.3	+	+	+	-	-	-	-
M. corticolus	1.7				+	+	+	-	-	+	-
Phycomyces nitens	0.5	3.2	1.6	0.5	+	+	+	-	-	-	-
Rhizopus nigricans	2.7			1.5	+	+	+	-	-	-	-
R. stolonifer	3.4				+	+	+	-	-	+	-
Zygorhynchus moelleri	0.5		1.7		+	+	+	[+]	-	-	-
Ascomycetes											
Chaetomium sp.		1.8			+	+	+	+	-	-	-
Nectria sp.		OC	OC	1.6	+	+	+	-	-	+	-
Penicillium luteum (series)		1.5	OC	1.6	+	+	+	-	-	-	-
Sordaria sp. (GL 32)	1.0	0.5			+	+	+	+		-	
Sporormia sp. (GL 37)		OC	0.5	OC	+	+	-	+	-	-	-
Fungi Imperfecti											
Alternaria tenuis (var.)	1.0	3.2	2.8		+	+	+	-	-	-	-
Aspergillus clavatus	2.3		1.6		+	+	+	+	-	-	-
A. flavus	OC	1.6	1.6		+	+	+	+	-	-	-
A. niger	2.3	2.3	1.6		+	+	+	-	-	-	-
A. ochraceous	1.6			1.5	+	+	+	-	-	-	-
A. versicolor	4.6		0.5	1.6	-	+	+	-	-	-	-
Aureobasidium pullulans			0.5	0.5	-	+	+	-	-	-	-
Botrytis cinerea	3.3	0.5	1.6	3.2	-	-	+	+	-	+	-
Cercosporidium graminis		1.5	OC		+	+	+	-	-	-	-
Cephalosporium acremonium		1.6	1.6	OC	+	+	+	+	-	-	-
Chalaropris thielavioides		1.3	0.5	0.5	+	+	+	-	-	+	-

Chrysosporium pannorum			1.7	2.3	+	-	+	+	-	-	-
C. pruinosum	1.2	OC			+	+	+	(+)	-	-	-
Cladosporium herbarum	9.5	1.6			+	+	+	-	[+]	[+]	-
C. cladosporoides	2.8	2.3	5.6	1.7	+	+	+	-			-
C. macrocarpum (var.)			OC		+	+	+	-	-	+	-
Cylindrocarpon sp. (GL 23)		1.0	OC	1.0	+	+	-	+	+	+	+
Cylindrocephalum sp. (GL 7)		1.3	0.5		+	+	-	+	-	+	+
Epicoccum purpurascens	2.7	OC			-	-	-	+		+	
Fusarium anguioides	OC	1.0			-	+	+	+	-	-	-
F. avenaceum	OC	1.6	2.3	1.6	+	+	-	-	-	-	-
F. culmorum	OC	OC	1.6		+	+	+	+	-	-	-
F. gramineum	OC	1.7	1.6	OC	+	+	-	+	-	-	-
F. nivale	OC	OC	OC	1.0	+	+	+	+	-	-	-
F. oxysporum		1.7	1.0	4.6	+	+	+	+	-	-	-
F. peae		5.6	1.7	1.7	+	+	+	-	-	-	-
F. roseum			OC	2.3	+	+	+	+	-	-	-
F. sambucinum		1.0	OC	5.6	-	+	+	+	-	-	-
F. solani (?)	OC	OC	2.8	OC	+	+	+	+	-	-	-
Fusarium sp.		OC	OC	OC	+	+	+	-	+	+	+
Fusidium sp.			1.3	OC	-	+	-	-	-	-	-
Gliomastix sp.			4.3	OC	+	+	+	-	-	-	-
Monilia sp.		1.0	OC	1.7	-	+	-	+	-	-	-
Nigrospora sp.		OC	0.5	1.0	+	-	-	-	-	-	-
Penicillium canescens		1.3	1.0	OC	+	+	-	-	-	-	-
P. citrinum	OC	1.0	0.5		+	+	+	-	-	-	-
P. claviforme			0.5	4.6	+	+	+	-	-	+	-
P. chrysogenum			OC	OC	+	-	+			+	
P. diversum			0.5	0.5	-	+	-	-	-	-	-
P. expansum			4.6	0.5	+	+	-	-	-	-	-
P. frequentens	3.0	0.5	2.3	OC	-	+	+	-	-	+	-
P. jantinellum		1.3	0.5	OC	-	+	+	-	-	+	-
P. genseni	2.2	5.6			+	+	-	-	-	-	-
P. lilacinum		0.5	1.0	OC	+	+	-	-	-	-	-
P. notatum	0.5		0.5		-	+	-	-	-	-	-
P. rugulosum	2.8	OC			+	+	+	+	-	-	-
P. stoloniferum	2.8	1.3		OC	+	+	+	+	-	-	-
P. thomii	2.4		0.5		-	-	-	+	-	-	-
Penicillium sp. (GLP 17)			0.5	1.3	+	+	+	-	-	-	-
Phialophora fastigiata (group)	1.5	2.3	1.5	0.5	+	+	+	+	+	-	-
P. cf. malorum	0.5	3.5		0.5	-	+	+	+	+	+	+

Table 1 (Continued)

Organisms	Standing dead in phyllosphere	Litter	Soil 0-10 cm	Soil 10-20 cm	Activity on: Pectin	Starch	Xylan	Cellulose	Humic acid	Gallic acid	Wooden dowels (lignocellulose)
Phialophora sp. (GL 106)	0.5	OC				+	+	+		+	
Phoma glomerata		1.0	2.6		+	+	+	+	+	+	+
P. cf. *herbarum*	OC	0.5	OC		+	+	-	-	+	+	-
Rhizoctonia sp. (GL 111)			2.6	2.8	-	+	-	+	-	-	-
Rhizoctonia sp. (GL 112)			OC	0.5	+	+	-	+	-	-	-
Scopulariopsis sp.			1.0	2.6	-	-	-	+	+	+	+
Sporobolomyces roseus	4.6	OC			-	+	+	-	-	-	-
Stachybotrys sp. (GL 41)	OC		0.5		+	+	+	(+)	+	+	+
Torula sp. (GL 88)	OC	1.6			-	+	-	-	-	-	-
Trichoderma koningii	1.0		0.5	OC	+	+	+	+	-	+	-
T. viride	0.5	1.5	1.0	OC	+	+	-	(+)	-	-	-
Trichoderma sp. (GL 93)	1.7	OC		2.8	+	+	+	-	-	-	-
Wardomyces sp. (GL 81)		0.5	0.5		+	+	-	-	-	-	-

Mycelia Sterilia											
Hyaline											
GL 1 (with clamp connection [CC])		OC	OC	2.8	+	+	+	+	-	-	+
GL 6	6.7				+	+	+	-	-	-	-
GL 11 [CC]		11.7	2.3		+	-	+	-	-	+	-
GL 18			2.3		+	+	-	-	-	-	-
GL 74		4.6	OC		+	+	+	-	-	-	-
GL 62			1.0		+	-	-	-	-	+	-
GL 102 [CC]		1.0			+	+	+	-	-	-	-
Dematiaceous											
GL 15	4.6		OC		-	+	+	-	-	-	-
GL 27 [CC]		1.0		4.0	+	+	-	+	+	+	+
GL 28			OC	4.6	+	+	-	+	+	+	+
GL 96 [CC]		2.3	1.0		-	+	+	-	-	-	-
GL 116				4.6	+	+	-	+	+	+	+
GL 126				1.6	-	-	-	+	+	+	+
GL 127		2.3			+	+	+	-	-	-	-

[a]Key: OC = occurs infrequently; + = positive at room temperature only; [+] = very weak + reaction; - = no activity; (+) = positive activity at room temperature and below 5°C.

[b]Activity blank = no test done; source blank = no occurrence.

Table 2 Taxonomy, utilization potential, and frequency (%) of fungi in taiga birch forests[a]

Organism	Activity					Frequency			
						Birch		Spruce	
	Cellulose	Gallic acid	Humic acid	Pectin	Starch	S	L	S	L
PHYCOMYCETES									
Mucorales									
Mortierella parvispora	-	-	-	-	+	2.4	4.7	1.7	2.6
M. ramanniana	+	-	-	+	+			1.3	0.6
M. ramanniana var. *angulispora*	-	-	-	(+)	(+)	6.7	16.1	4.1	4.6
M. verticillata	-	-	-					1.0	
M. vinacea	-	-	-	+	+	5.5	3.5	11.7	0.3
Mucor corticolus	-	-	-	+	+	0.4		0.5	
M. microsporus	-	-	-	+	+	2.1	8.0	1.3	5.0
M. mucedo	-	(+)	-	(+)	(+)	1.2	6.3	0.3	3.3
M. saximontensis	-	-	-	+	+	8.7	2.5	14.4	5.3
ASCOMYCETES									
Sphaeriales									
Eupenicillium sp. F-27	+	-	-	-	+	0.2		5.5	0.6
Mycosphaerella cf. *tassiana*	-	+	+	-	+	1.2		0.3	
Hypocreales									
Nectria viridescens	-	(+)	+	(+)	(+)	0.2		2.7	1.0
FUNGI IMPERFECTI									
Moniliaceae									
Acremonium sp. F-120	(+)	-	-	(+)	+		2.0	0.3	
Aureobasidium pullulans	-	-	-	(+)	+			1.7	
Calcarisporium arbuscula	-	-	-		(+)	0.2	0.7		

Chrysosporium cf. *merdarium*	(+)	-	-	(+)			0.6		
C. pannorum var.	-	-	-	(+)	-	0.2	0.3		
C. pruinosum	+	-	(+)	-	+	0.4	0.2		
Penicillium cinereo-atrum	-	-	-	+	(+)	9.4	4.5	1.0	2.0
P. claviforme	-	+	-	+	+		0.3	1.0	6.0
P. daleae	-	-	-	+	+		0.2		
P. duclauxii	+	-	-	+		0.2	0.2		1.0
P. funiculosum	-	-	-	+	+				2.0
P. implicatum	+	-	-	+	+		0.3		1.0
P. pinetorum	-	(+)	-	-	+		0.3		
P. raistrickii	-	-	-	(+)	+	1.2	5.5	1.0	13.0
P. stoloniferum	-	-	-	+	+		2.2	1.0	2.6
P. thomii	(+)	-	-	-	+		1.0		
P. variabile F-140	+	-	-	+	+			1.3	
Penicillium sp. F-90	+	+	-			0.4		1.0	0.6
Penicillium sp. F-144	-	-	-	+	+	0.2			
Tolypocladium inflatum	-	-	-	+	+	18.1	10.0	10.0	6.0
Trichoderma polysporum	-	-	-	+	+	9.4	11.8	1.0	16.3
T. viride var. F-34	+	-		+	+	2.4	3.2	3.1	9.7
T. viride var. F-78	+	-	-	+	+	7.0	5.2	4.8	6.3
T. viride var. F-132	+	-	-	+	+	2.4	4.7	3.7	6.6
Trichoderma sp. F-2	-	-	-	+	-	1.4	0.5		0.3
Dematiaceae									
Cladosporium herbarum	-	+	+	+	+	0.2	0.5	1.3	
Oidiodendron griseum	-	+	-	+	+		0.2		
Phialophora hoffmanni	+	-	-	+	+	5.0	0.2		
P. cf. *malorum*	+	+	+	-	-		0.2	0.6	
P. malorum	+	+	(+)		+		0.2		
Stachybotrys atra	+	+	-	+	+	1.2	0.2	1.0	
Torula sp. F-119	-	+						0.3	
Sphaerioidaceae									
Ceuthospora cf. *phacidibides*	+	-	-	-	+	8.4	0.5		
Phoma sp. PB-8	+	+	-	+	+		0.2		

Table 2 (Continued)

Organism	Activity					Frequency			
						Birch		Spruce	
	Cellulose	Gallic acid	Humic acid	Pectin	Starch	S	L	S	L
Excipulaceae									
Pilidium acerinum	-	+	-	-	-	0.2	0.7		
Tuberculariaceae									
Fusarium roseum	-	-	-	+	-		0.2		
MYCELIA STERILIA									
Mycelia sterilia F-13	+	+	+	-	+			0.6	
Mycelia sterilia F-62	-	-	-	+	-			1.0	
Mycelia sterilia HC-12	-	+	+	-	-	1.4	1.2	0.3	0.6
Sclerotium sp. F-41	+	+	-	+	-		0.2	1.3	
Sclerotium sp. F-79	+	+	-	-	-			2.0	

[a]Activity blank = no test done; source blank = no occurrence.

gi in the aspen site were not significantly different from those reported here for the birch forest. The isolates from the latter sites were identified by the gross characteristics of their growth on agar plates as compared with known isolates, given a culture number, and tested for enzyme activity as described earlier (Sec. II.B).

Fungal species diversity, as measured from fungi isolated on agar plates, decreased markedly between the temperate grassland sites and the high arctic grassland sites, where, respectively, 131 and 38 species were isolated. The temperate peat bog site contained approximately 95 species. The birch, spruce, and aspen forest sites and the alpine tundra site at Eagle Summit contained 48, 42, 50, and 28 species, respectively. Microbial species diversity in all groups including bacteria, yeasts, basidiomycetes, and fungi in general in the northern sites is very low relative to that in other biomes (Bunnell et al., 1980). The results of this study support the view that fungal species diversity decreases in the latitudinal gradient from temperate to arctic ecosystems and that species diversity increases with less variable climate.

Seasonal changes in fungal distribution patterns were not detected at any of the sites studied. The lack of seasonal colonization patterns for fungi had been observed earlier for tundra by Flanagan and Scarborough (1974) and for a forest podzol by Williams and Parkinson (1964). However, many significant within-site differences in taxa were obvious between the mycofloras of the phyllosphere, litter, and soil horizons. This spatial segregation of fungal taxa probably reflects the timecourse of successional changes which would be observed if standing dead leaves or litter were examined over a period of several years. Other studies in which this was done have provided clear evidence for fungal succession (Webster, 1956, 1957; Watson et al., 1974).

Many obvious taxonomic differences are seen between the mycofloras from different sites (see Tables 1 and 2; also Flanagan and Scarborough, 1974; Dowding and Widden, 1974; Bunnell et al., 1980). The major differences involve a scarcity or absence of certain genera (*Alternaria*, *Aspergillus*, *Botrytis*, *Fusarium*, and *Rhizopus*) from the higher latitude sites. Further, in northern forests and in tundra sites respectively *Trichoderma* and *Penicillium* spp. are not numerous, apparently replaced by greatly increased numbers of *Mycelia sterilia* (Flanagan and Scarborough, 1974).

B. Fungal Enzyme Activity

Starch, pectin and xylan were degraded by more than 65% of fungi in all ecosystems studied; no significant differences in fungal abilities to utilize these polysaccharides were noted for any site. Mycofloral utilization capacity decreased in the order pectin, starch, xylan (equally), cellulose, gallic acid, humic acid, and lignocellulose (wood) in all study sites. Across the ecosystems studied the percentages of fungi capable of utilizing pectin, starch, xylan, cellulose, humic and gallic acids, and wood were 65-98%, 78-95%, 65-96%, 22-28%, 11-17%, and 4-10%, respectively.

In general, the variation in specific hydrolytic potentials at room temperatures expressed as a percentage of isolated mycofloras between different sites was no greater than the variation in the same potential measured within a site at different times. Statistical analysis showed no significant between-site differences at the 5% level.

Forest ecosystems were expected to, but did not have, proportionally more cellulose and phenolic acid-degrading fungi. Forest mycofloras did have slightly higher average percentages of lignocellulose decaying fungi. However, statistical treatment of variation in this capacity within a site in a given year and between sites showed no significance at the 5% level.

C. Spatiotemporal Mycofloral Utilization Capacities

During the summer season at each site the percentage of fungi isolated having a specific capacity to hydrolyze plant structural constituents did not vary significantly. Although sites showed no seasonal successional pattern for mycofloral decay capacities, pronounced differences in such capacities were noted at different depths in the soil profile and in the phylloplane (Figs. 2-4). In the four sites studied in detail (Pt. Barrow tundra, Eagle Summit tundra, and the temperate peat bog and grassland sites), the proportion of cellulolytic and lignocellulolytic fungi in the resident microbial populations increased with increasing depth in the litter and soil. Phylloplane microbial populations contained a lower proportion of these fungi than did any of the soil microbial populations. Similar distribution patterns were observed for fungi capable of hydrolyzing pectin, starch, and xylan (Figs. 2-4).

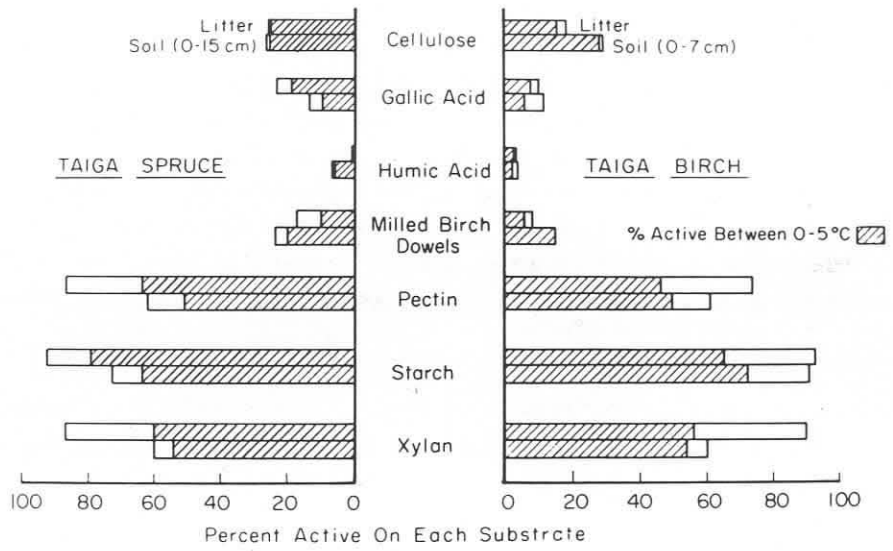

Fig. 2 Distribution by site and forest floor horizon of fungal enzyme capabilities at room temperatures and below 5°C.

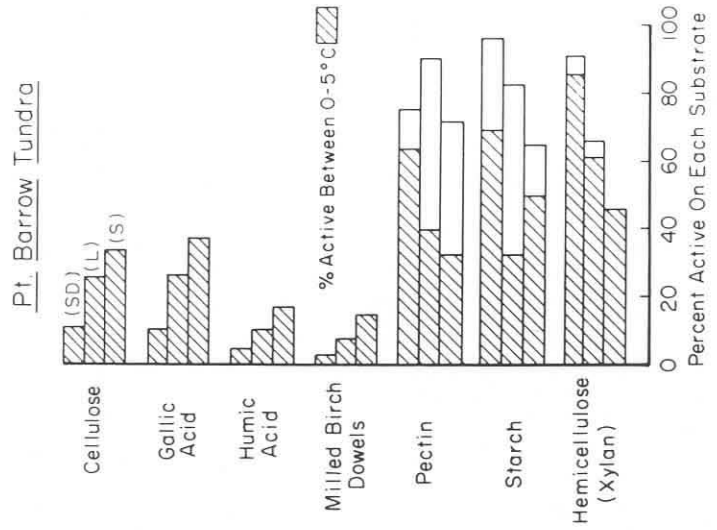

Fig. 3 Spatial distribution of fungal enzyme capability at room temperature and below 5°C in arctic tundra. Key: SD = standing dead vegetation in phyllosphere; L = litter; and S = soil 0-10 cm. (From Bunnell et al., 1980.)

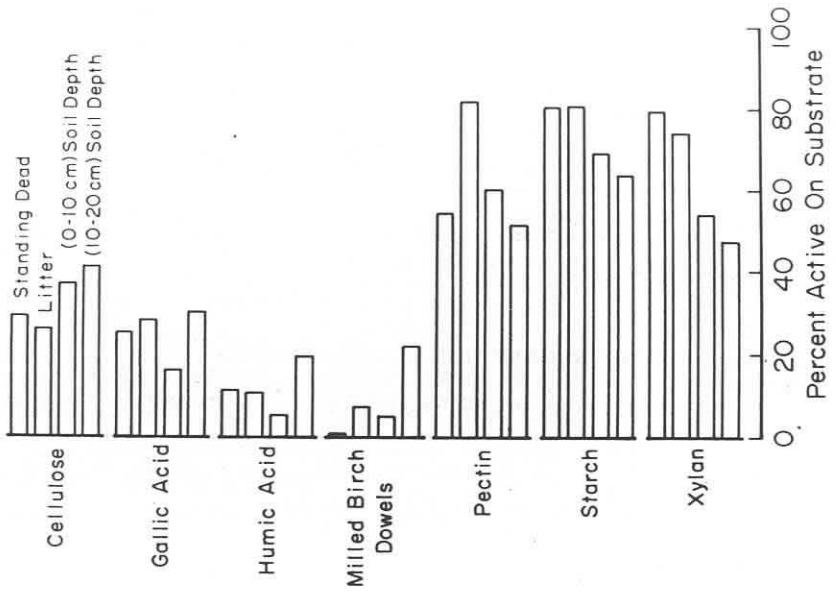

Fig. 4 Spatial distribution of fungal enzyme capability at room temperature in a temperate grassland site. Fungi capable of breaking down substrates at temperatures below 5°C were few, and results of tests were often dubious.

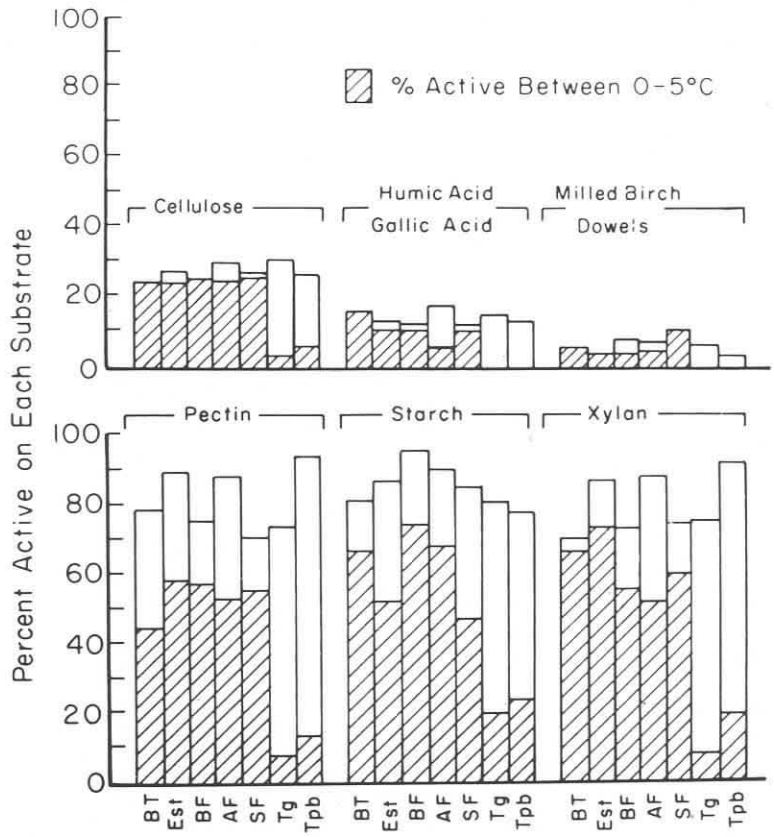

Fig. 5. Between site comparison of the percentage of fungi at each site capable of hydrolyzing the test substrates at room temperature and below 5°C. Data presented are based on tests performed on fungi isolated in midsummer season over a period of 6 years (BT, Barrow tundra; Est, Eagle Summit tundra), 5 years (BF, birch forest), 4 years (SF, spruce forest), 2 years (AF, aspen forest; TPb, temperate peat bog), and 1 year (Tg, temperate grassland). Within-site seasonal variation in a hydrolytic capacity and between-year variation within sites was greater than the between-site variation in hydrolytic capacity illustrated in the figure.

D. Temperature and Fungal Substrate Utilization Capacities

In marked contrast to the tundra and taiga mycofloras, the temperate ecosystem fungi showed very little capacity to decay any of the test substrates below 5°C. Low temperature (below 5°C in vitro) rendered the temperate site fungi inactive on humic acid, gallic acid, and birch wood and almost obliterated their potential to decay cellulose, pectin, starch, and xylan (Fig. 5). In the more northern sites fungi retain some capacity to utilize all test substrates below 5°C, albeit at reduced rates, but cold does not completely stop any of these activities until temperature drops below 0°C.

However, in all the northern sites a percentage of fungi do cease to be active on a given substrate at low temperature. This tendency is more pronounced with pec-

tin, xylan, and starch than it is with cellulose and lignin compounds. All of the fungi from Pt. Barrow tundra retain some capacity to utilize cellulose and lignocellulose down to -2°C, but the percentage of fungi capable of utilizing pectin, starch, and xylan decreases by 35%, 14%, and 3%, respectively, below 5°C. The tendency for fungal populations to show decreased activity at low temperatures on pectin, starch, and xylan to a significantly greater degree than on lignocellulose and cellulose compounds was observed in all the northern sites (Figs. 2 and 3).

Another tendency related to fungal spatial position in the ecosystem is seen in the northern sites and particularly the northern forest sites. In these sites the proportion of fungi capable of utilizing pectin, starch, and xylan at low temperatures increased with increasing depth in the soil profile (Figs. 2 and 3). This tendency is also seen, though not as clearly, with fungi capable of degrading cellulose or lignocellulose. In examining the temperate grassland mycoflora, no similar relationships were observed (Fig. 4).

None of the fungi tested at any of the sites were specialists to the extent that they used only one substrate.

At room temperature no significant differences in fungal substrate utilization capabilities were seen, either within sites or between sites (Fig. 5). At low temperatures highly significant differences were seen between the substrate utilization capacities of fungi from northern sites and those from temperate sites (Tables 1 and 2). The within-site variability in fungal capacity to decay a given substrate at 2-5°C was also highly significant. But between the northern sites there was no significant difference in mycofloral utilization potential at low temperatures (Fig. 5). These data clearly indicate a low-temperature accomodation of the enzymes in fungi from the northern sites which barely exists in fungi from temperate climes. Clearly the temperature range wherein northern fungi may be active on a given substrate is much broader, because the optimum temperature for activity of many of these northern fungi is close to 40°C but the low temperature threshold is extended to 0°C or even to subzero temperatures (Flanagan and Veum, 1974). The broader range for mycological activity in northern ecosystems is consistent with the greater extremes of temperature experienced in the northern ecosystem (Table 3).

The vast majority of fungi utilized starch, pectin, and xylan with more or less the same level of efficiency. The *Phialophora* and *Phoma* isolates were the most versatile, being capable of vigorous growth on all substrates. Only a few sterile forms, which because of clamp connections were probably basidiomycetes, shared this versatility.

E. Fungal Biomass

In this study fungal biomass as expressed in meters per gram DWS, almost always decreased with depth. Expressed in grams per square meter, fungal biomass varied widely between sites (Table 4). When results were expressed in meters per gram of organic matter (OM), the decrease in fungal biomass with depth was not marked; in fact it

Table 3 Climate and cellulose decomposition[a]

Site	Dates (years studied)	Percentage weight loss ($\pm S_x$)	pH	Mean annual temp. (°C)	June 15 - Sept. 15 max.	min.	mean
BT	June 15-Sept. 15 (1970-75	3.8 ± 0.3	5.0	-12.5	12.7	-2.0	5.2
Est	June 10-Sept. 15 (1970-75)	3.4 ± 0.5	5.5	-21.0	22.5	-4.5	8.3
BF	June 30-Oct. 15 (1971-75	5.2 ± 1.3	6.0	-20.0	32.0	4.0	16.1
AF	June 5-Sept. 20 (1976-77)	5.0 ± 2.0	6.3	-16.0	31.6	5.3	17.2
SF	June 30-Sept. 30 (1972-75)	3.4 ± 1.0	4.4	-23.0	32.0	5.5	16.3
Tg	May 30-Sept. 10 (1973)	4.2 ± 1.1	6.7	10.5	24.3	8.2	14.7
TPb	May 25-Sept. 11 (1973-74)	3.8 ± 1.7	4.5	10.0	23.7	9.2	12.8

[a]Watman No. 1 cellulose strips were used. (See the text.)

often increased with depth, especially in the highly organic soils (Table 5).

By expressing fungal biomass in meters of live hyphae per gram OM, differences between most of the sites for similar layers (0-5 cm and 5-10 cm) disappeared (Table 4). The notable exception to this observation was the black spruce forest live fungal biomass. The reason for this exception will be discussed later. Apparent differences between sites in the 0-10 cm horizons when fungal biomass is expressed as meters per gram DWS, meters per gram OM, or grams per square meter all disappear when the fungal biomass is expressed as meters of live mycelium per gram OM. It seems that between-site differences in fungal biomass are due primarily to differences in amount and density of organic matter in the upper 10 cm of organic soil and to the fact that the proportion of live to dead mycelium varies significantly between sites and between horizons within sites (Table 4).

The regression of grams of live mycelium versus kilograms per square meter OM above mineral soil irrespective of organic layer depth (Fig. 6) shows a strong significant correlation between organic matter content and grams of live mycelium per square meter. If the taiga spruce forest and the temperate peat bog data are removed from the set, the fit of the regression line is extremely good and so we can venture to say that in sites other than these there is approximately 1.0 g of fungal tissue per kilogram OM. This relationship does not hold for the black spruce site nor for the temperate peat bog organic soil, possibly due to the poor quality of fungal substrates in both sites (Table 5). That both sites contain considerable amounts of sphagnum moss remains may also be significant in this regard since this moss decomposes very slowly and in general accommodates few fungi or bacteria (P. W. Flanagan, unpublished data). The high tannin, acidic, and humic content of the organic matter in these sites, together with resin, waxes, cutin, and gums in the black spruce site,

Table 4 Average live and dead fungal biomass in site horizons[a]

Site	Depth	Biomass (m/g DWS)	Biomass (m/g OM)	Meters of live mycelium per gram OM	Meters of dead mycelium per gram OM	Grams live mycelium per m^2 to mineral soil (cm)
Pt. Barrow	0-5	774	793	487	306	16.2(12)
	5-10	473	804	463	341	
Eagle Summit	0-5	660	676	427	249	7.5(8)
	5-10	312	614	477	137	
Birch forest	0-5	450	542	435	107	3.5(7)
	5-7	203	721	503	218	
Aspen forest	0-5	510	600	518	82	5.8(9)
	5-7	210	735	476	258	
Spruce forest	0-5	225	246	228	18	4.6(25)
	5-10	300	322	307	15	
	10-15	262	282	221	46	
Temperate grassland	0-5	536	687	544	143	6.5(10)
	5-10	202	663	558	105	
Temperate peat bog	0-5	494	537	438	99	16.5(35)[b]
	5-10	654	719	414	305	
	10-15	754	810	245	665	
	15-20	825	840	102	738	
	20-25	1177	1206	144	1062	
	25-30	696	717	87	630	

[a]Above the mineral soil from June to September.

[b]As far as measurements were made; mineral soil was not encountered in this site until the 1.5 m level.

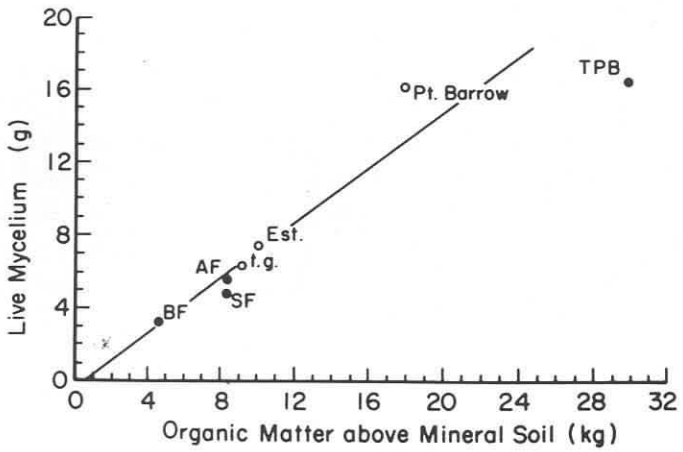

Fig. 6 Regression of grams of live fungal biomass by site against each site's organic matter content (n = 7, r = 0.90).

Table 5 Results at the various sites in terms of organic matter

Site	Kilograms per square meter of organic matter to mineral soil	Percentage of organic matter readily extractable[a]	$\bar{x}$ (mg/m^2) Soluble N	$\bar{x}$ (mg/m^2) Extractable P
Eagle Summit	10.5	14.5	118.5[b]	7.4[b]
Pt. Barrow	18.0	13.5	3600.0[c]	22.0[c]
Birch forest	4.3	14.8	422.0	188.0
Spruce forest	8.6	2.5	166.0	31.0
Aspen forest	8.2	12.8	215.0	165.1
Temperate grassland	9.0	11.7	566.0	160.5
Temperate peat bog	29.0[d]	3.3	192.0[e]	17.5[e]

[a]Warm water followed by 80% ethanol.

[b]From Anderson (1974).

[c]From Chapin et al. (1978).

[d]To 35 cm, mineral soil not encountered.

[e]Upper 10 cm.

all increase the recalcitrance to organic decay, paucity of fungal biomass, and low availability of essential nutrients (Table 5).

IV. SUMMARY AND DISCUSSION

There was very low substrate specificity among all the fungi (>400) tested, and at room temperature few differences existed among species for utilization of a given substrate, even among those from geographically widely separated sites. Between northern sites there was no significant difference in mycofloral substrate utilization potential at low temperatures, but between northern and temperate zone sites such differences proved extremely significant.

What is lacking here is a measure of the content of each test substrate between study sites. However, the measurement of "readily soluble" substrates between sites (Table 5) is positively related to the live fungal biomass measurements.

The residence of fungi in soils is the organic matter matrix. The data presented here indicates that this niche on average is occupied by 0.5-1.0 g dry weight of living fungal biomass per kilogram OM (Fig. 6) irrespective of site latitude. The biomass present is related positively to organic matter quantity, and the data indicate that there is a further positive relationship between substrate quality and fungal biomass.

Fluctuations in fungal biomass within a site are most readily explained in terms of input of organic matter in spring and fall (Bunnell et al., 1980; Söderström, 1977)

and to variations in site temperature and moisture (Flanagan and Van Cleve, 1977). From the limited data available, the seasonal fluctuation (increases and decreases) about the mean midseason fungal biomass seems to be by about two to three times. Lower degrees of fluctuation, i.e., twofold or less, are associated with the lower-quality organic remains (Flanagan and Van Cleve, 1977; Söderström, 1977) and the higher fluctuations are associated with the higher quality substrates, e.g., tundra litter and standing dead remains (Bunnell et al., 1980). Apparently, not only is the average fungal biomass controlled by substrate quality, but also the amplitude of seasonal fluctuations in biomass within a substrate is controlled by its quality; hence seasonal fungal productivity in a site is controlled by substrate quality.

The component species of this biomass of enzyme-secreting fungal network, though varying from site to site, do not seem to affect the process of decomposition in the field, at least as far as cellulose is concerned (Table 3). The tundra sites do not appear to accumulate organic matter (Flanagan and Bunnell, 1978) any more than the temperate grassland or northern deciduous forest sites do. The peat bog site, basically a graminoid/sphagnum-dominated wet site, does accumulate organic debris, as do the black spruce forests of interior Alaska.

Although only seven sites were studied, the data suggest that the main determinants of fungal biomass in these ecosystems are the quantity and quality of organic matter. It seems that the temperature differences between sites do not influence fungal biomass per gram OM and furthermore that, irrespective of site climatic conditions, if organic quality and availability of inorganic nutrients (Table 5) is low, fungal biomass will be proportionally low. These observations indicate a temperature adaptation of some members of the fungal community enabling them to fill the decomposer niche in northern climates (Flanagan, 1978) and an inability of fungi to exploit certain kinds of substrates irrespective of site climate differences.

The low fungal species diversity in northern ecosystems whether gramineous or forest is to be expected and has been commented on previously (Dowding and Widden, 1974; Bunnell et al., 1980). The cause for this low fungal species diversity is unclear, but it may be related to an inability in most soil fungi to adapt to low temperatures and/or to the fact that tundra systems are geologically young and have not as yet received their full complement of organisms. The observation that certain cold-tolerant fungi represent a large portion of the colonists of organic matter, e.g., *Tolypoclodium inflatum* (taiga forests), *Cladosporium herbarum*, and sterile mycelium (tundra; see Flanagan and Veum, 1974) and that many northern fungi are *psychrophilic*, or cold tolerant (Flanagan and Scarborough, 1974; Bunnell et al., 1980; Flanagan, 1978), adds support to the view that the composite mycological niche in tundra is occupied by cold-adapted fungi.

The strikingly high proportion (frequency sum) of *Trichoderma* sp., *Tolypoclodium inflatum*, *Penicillium* spp., and *Mucor* spp. in the northern forest sites is noteworthy, as is the absence therein of *Fusarium* sp. and other soil fungi such as *Botrytis*, *As-*

pergillus, and *Rhizopus*. The high proportion of sterile forms in tundra sites further accents generic and specific differences in the fungal flora between sites.

Despite these differences, however, the data from cellulose decay measurements, live biomass measurements, and analyses of decomposer potential between sites (Fig. 5) support the view that there is a decomposer system attuned to each ecosystem which ensures that decomposition goes on at a rate commensurate with the rate of primary production. Thus, these data suggest that the size of the composite niche occupied by fungal decomposers in ecosystems is determined directly by the quantity and quality of the primary production (see also Lockwood, Chap. 18). The diversity in fungal niche occupants seems to be related to climate and decreases with increasing latitudes. Fungal versatility in enzyme production and cold tolerance may compensate for lack of species diversity in northern climates. The obvious low-temperature tolerance of most northern fungi and the inability of most temperate fungi to function at near-zero temperatures helps explain how the fungal niche in northern ecosystems is filled and how the process of decomposition is sustained.

It appears that taxonomic differences in fungal communities between ecosystems do not significantly influence the decay rate of plant remains between sites. The biomass of fungi is related to quantity and quality of organic matter, and the decay rate of a given organic matter is controlled primarily by climate. In northern ecosystems with adverse climates the fungal decomposer niche comprises fungi with low-temperature adaptation and wide separation between minimum and maximum temperature thresholds.

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